

A NEW FAMILY OF ENSIFEROUS ORTHOPTERA FROM THE COASTAL SANDS OF SOUTHEAST QUEENSLAND

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ABSTRACT

A new family, Cooloolidae, of Orthoptera is proposed, based on a single new genus and species *Cooloola propator* Rentz, from southeast Queensland, Australia. The cricket-like insect, referred to as the Cooloola monster, is an aberrant member of the suborder Ensifera. It is unusual in possessing very short antennae which, in turn, have a reduced number of articles, 10 in number. Nearly all species in all families of Ensifera have antennae with 30 or more articles. The structure of the mouthparts is unique in the Orthoptera in that the lacinia of the maxilla is larger and more developed than the mandibles. The lacinia is knife-shaped and not hooked. This suggests a piercing rather than the usual sorting and cleaning function for that structure. The mandible is elongate, indicative of a predaceous habit as opposed to short, stout mandibles which are possessed by plant feeders. *C. propator* has no close relatives but superficially resembles several species of the stenopelmatid *Oryctopus*. This genus is known from south India and Ceylon. Both genera share modification for a burrowing habit as illustrated by shortened antennae and legs, excavate, trowel-like modified spines, pale coloration, reduced eyes, and brachypterous males and apterous or micropterous females. The tarsal claw of both genera is sexually dimorphic. In females it is greatly reduced but normal in males. This may indicate a more sedentary role for females. Detailed examination of mouthparts, alimentary tract, and wing venation reveal that *Oryctopus* possesses all of the characteristic structures of the Stenopelmatidae, whereas *Cooloola* does not. The convergence of characters is interpreted as adaptation to a fossorial existence.

Cooloola propator lives in sandy, moist soils and is not particularly associated with a single vegetation type. In rainforest and open forest, the soil is densely laced with roots. There is little accumulated litter on the surface and the soil is devoid of humus. The sand is usually bare and moist. Wandering adult males have been collected at night and their above-ground activity seems to be associated with wet weather. They appear to be active after periods of rain. Females are apparently completely subterranean.

Every taxonomist is at first sceptical, and, hopefully, subsequently convinced of the reality of a new family of organisms. In an insect order such as the Orthoptera (grasshoppers, crickets, and allies), such an occurrence is extremely rare. This order is conservatively structured at the family level, despite recent escapades of several authors into the field of taxonomic escalation (see Kevan, 1977, for review). The last time a family was proposed based on an entirely new taxon was when E.M. Walker (1914) described the Grylloblattidae as a new family of Orthoptera.

This paper describes a new family of cricket-like insects, the only known representative of which is known popularly as the 'Cooloola monster'. The history of the discovery is traced, and various structures are compared with those in other Orthoptera.

The new family Cooloolidae is placed in the superfamily Gryllacridoidea based on its similarities with *Oryctopus* of the Stenopelmatidae. Although *Cooloola* Rentz gen. nov. is highly specialized in many characters, it can be assigned to the Gryllacridoidea on the basis of its tarsal formula and structure, lack of tegminal stridulatory structure, and general appearance.

HISTORY OF THE DISCOVERY OF THE COOLOOLA MONSTER

Shortly after arriving at my new post as Curator of Orthoptera, CSIRO, Canberra in 1977 I was presented with a small parcel from Mr E.C. Dahms, Curator of Insects, Queensland Museum, Brisbane with a note 'Here's something to introduce you to the Australian fauna'. After some amusement at the technical excellence of the

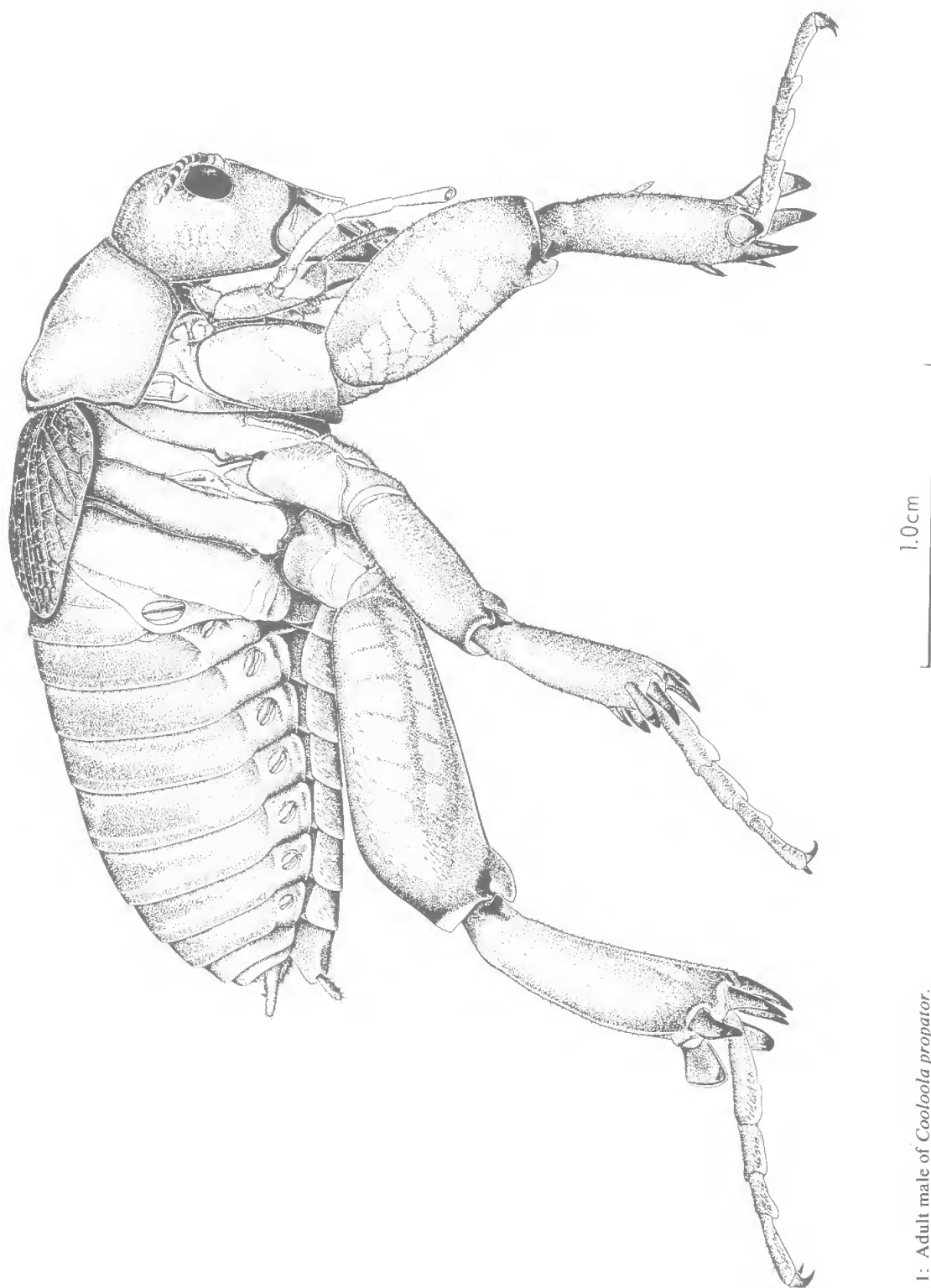


FIG. 1: Adult male of *Cooloolola propator*.

apparently manufactured monster, it was determined that it was a genuine complete cricket-like insect.

The specimen had been taken by Dr V. Davies, Curator of Arachnids, Queensland Museum, in a pitfall trap set in mid-February 1976, in the rainforest of Cooloola National Park, near Gympie, Queensland. It was an adult male. A field trip to the area was planned and in the company of my wife, Mr E.C. Dahms, Mr I.D. Galloway and Dr G.B. Monteith, nearly two weeks were spent searching for the insect, but to no avail. All sorts of techniques, including digging, night searching, pitfall trapping and the oatmeal trail were used but no further specimens were located.

Subsequently a popular article concerning the interesting discovery was prepared for the news media. The article received wide circulation and had a photograph of the insect, dubbed the 'Cooloola monster'.

The second specimen, a small nymph, was collected on nearby Fraser Island by Mr T. Bade, a ranger from the National Park, on 1 July 1978. He recognised the insect from details given in the article in 'The Courier-Mail', and rushed the live specimen to the Queensland Museum, from where it was forwarded to me in Canberra.

Another trip was planned, at a different time of the year and including a few days on Fraser Island. The field work involved extensive digging and sieving soil, but the monumental efforts of those involved yielded no specimens.

Shortly after conclusion of the trip, another specimen, a live adult male, was brought into the Queensland Museum by Mr R. Nicholas. He had been camping at Freshwater Lake camping area, Cooloola National Park, and the insect crawled into his tent at dusk after a rainstorm. He recognised it as the one featured in 'The Courier-Mail' some 4 months previously.

The absence of females from the small samples was contrary to my experience with similar-looking Jerusalem crickets of the western United States. Adult males of these crickets are always difficult to obtain, and females and juveniles make up the bulk of collections (see Tinkham and Rentz, 1969, for discussion). The discovery of the fourth specimen, a female, possibly last instar nymph, ended conjecture. Its large, physogastric abdomen and short legs and tarsi indicate that the female is an obligate burrower and probably seldom walks on the surface of the ground. The specimen was found by Park Ranger Mr M. Johnston who dug it from a depth of 45 cm; the

site was within 50 metres of where Mr R. Nicholas found his specimen.

The fifth specimen, an adult male was collected by Ms K. Plowman in a pitfall trap in the vicinity of Lake Cooloola. The trap had been in the ground from mid October to mid November, 1978 when it was checked.

Mr Paul Nicholas was preparing camp one evening in Aug. 1979 1 km south of Freshwater Lake in the vicinity where his father had previously found a male in Oct. 1978, and discovered a struggling cricket killed by the wheel of his automobile. It had been apparently brought to the surface by the wheels of the vehicle.

The seventh specimen was found by Mr R. Perry, who was camping near Rainbow Gorge, Fraser Island in Oct. 1979. He found it while digging a shallow hole just above the beachline.

Gutter traps based on 3 m lengths of roof guttering set in the ground so as to drain into buried buckets of formalin were designed by Dr G.B. Monteith and the author and constructed by CSIRO Division of Entomology. These were installed at the Freshwater Lake camping ground on February 4, 1979. They were checked in early May, 1979, without success, but when they were terminated on January 28, 1980, one was found to contain 5 adult males of the new insect. It is significant that a full year's trapping of insects moving on the ground surface yielded neither females nor juveniles.

Mr E. Zillman, of Gin Gin, Queensland, who was formerly with the National Park service on Fraser Island, submitted photographs of an adult female he had found on Fraser Island in June 1978. The specimen was uncovered at a depth of 22 cm around the roots of a brush box tree (*Tristania* sp.). He has seen the Cooloola monster on more than one occasion but was not aware of its importance until recently. He found one female under *Banksia* logs in sandy soil at a depth of 30 cm in a compost heap 'some years before'. He is also convinced he dug one at Walla Lagoon, near Bundaberg, Queensland at 38 cm in 1952. Mr Zillman notes that his specimens were all found in sandy, and shaded soil, rich in surface roots. He considers the monster 'fairly common'.

ECOLOGY

Although ecological information is based on only 12 specimens, we can draw a number of conclusions regarding its habits and habitat preferences. The living specimens were observed to have a radically different gait from what one expects of a cricket-like insect. The actions of the

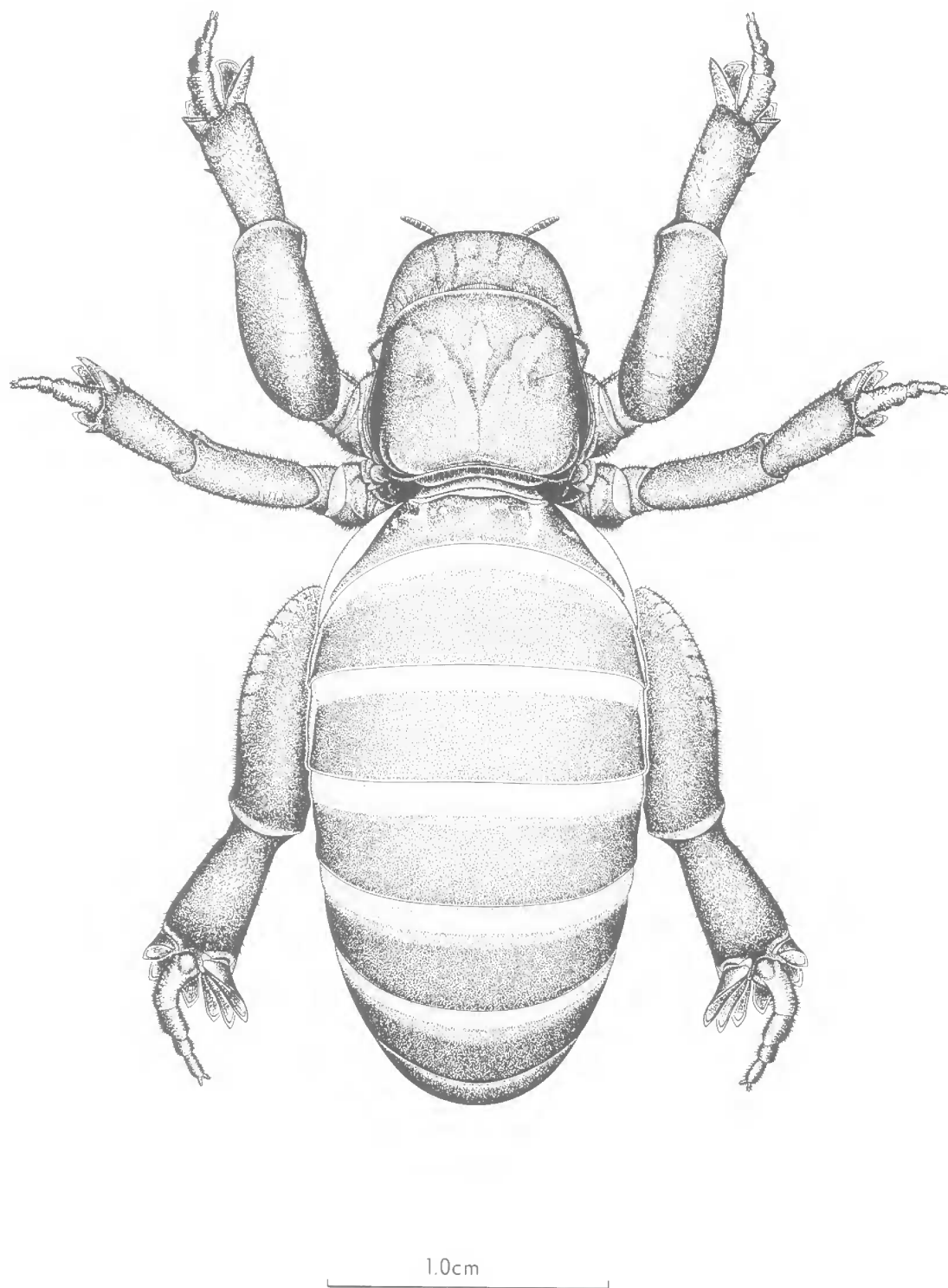


FIG. 2: Female of *C. propator*, subadult, see text.

monsters have been described as 'stomping' or tractor-like. The monster's movements are those of a fossorial creature out of its habitat. Males apparently venture forth, perhaps during rainy periods, in search of females. Otherwise they are subterranean. All specimens to date have been found within 45 cm of the surface, none deeper, although considerable digging to 3 m has been done. Mr Zillman's notes indicate the species may be associated with buried rotting wood.

Southern coastal Queensland from Coolangatta (just south of Brisbane) to Bundaberg and adjacent sandy islands, has been the subject of intensive continuous investigation by CSIRO Division of Soils and others. The area includes rainforests, sand dunes, and coastal heath habitats. It is well known locally because of the coloured 'rainbow sands'. A list of the twelve classes of landforms in the area was presented by Thompson (1975).

Watson and Arthington (1978) noted the restricted distribution of two dragonflies to acid dune lakes on Fraser Island and several other islands to the south. Ingram and Corben (1975) reported on four species of 'acid frogs' which breed only in water of low pH in wallum area of southeastern Queensland. These areas are within the range of the Cooloola monster. The wallum areas have apparently acted as islands during dry interpluvial periods. The discovery of *Cooloola propator* n. sp. in this rather limited but unique area is another indication that the habitat is peculiar and deserves protection.

The first Cooloola monster was collected from near Poona Lake, a habitat which corresponds to Thompson's Class 5, high transgressive dunes. This type of dune formation with elevations from 100-200 m is found at Cooloola, Fraser Island, and Moreton Island to the south. The dunes are formed from windblown sands from the adjacent beach. The high transgressive dunes support open forest and rainforest. The rainforest is restricted to bottoms and slopes of closed corridors, that is, dry valley bottoms. The other 11 specimens were found in Thompson's Class 4, yellow-brown transgressive dunes. These range from 30 to 60 m above sea level and have been formed from sands blown off the beaches relatively recently. This zone is relatively rich in minerals and supports moderately dense vegetation. The Cooloola monster has been found in both rainforest and open forest with 11 of the 12 specimens coming from the latter. On Fraser Island it has not yet been found in rainforest.

In areas where the insect has been found, the soil, to a considerable depth, is interlaced with tree roots. The sandy substrate is moist and there is little in the way of accumulated litter or humus on the surface. Large earthworms were not uncommon and their burrows extend to considerable depths. Other organisms were seldom encountered.

Family COOLOOLIDAE, new family

TYPE GENUS: *Cooloola*, new genus (Feminine gender)

CHARACTERISATION: The family Cooloolidae is unique among the families of Orthoptera in the following combination of characters.

Antennae reduced in length and number of articles.

Mandibles reduced in size relative to maxillae; in structure designed for grasping or tearing, not chewing; lacinia lanceolate, without hooks, designed for piercing.

Foregut extraordinarily long, extending nearly to apex of abdomen; proventriculus not highly modified, similar to the Haglidae.

Pro-, meso-, and metapleura dorso-ventrally expanded, presenting a highly 'muscular' appearance.

Legs highly modified, femoral shape and spination of tibiae sexually dimorphic, fore femur greatly expanded dorso-ventrally, in length subequal to hind femur (more nearly equal in female); fore and hind legs (excluding tarsi) of nearly equal length; middle legs less modified, more slender.

Tarsi very elongate, sexually dimorphic; in males very elongate, in females proportionately shorter; male tarsi weakly dorso-ventrally flattened, less so in female; male tarsal claws normal, in female reduced, minute, laterally compressed; all tarsi 4-segmented.

Tegmina present only on males, females apterous; tegmen highly sclerotized, convex, its caudal apex moulded around metathorax; tegmina separated dorsally, appearing to be capable of movement (perhaps used in burrowing); wing represented as minute, sclerotized bud.

Abdomen not highly modified in male, exceedingly bulbous in female; male cercus not suited for grasping, paraprocts platyform, each with dorsal hook; subgenital plate bearing styli. Neither sex with any kind of stridulatory apparatus.

Ovipositor short, 6-valved, not extending much beyond apex of abdomen; female subgenital plate very short, with digitiform caudal projection lying between ovipositor valves.

Cooloola Rentz, new genus

TYPE SPECIES: *Cooloola propator* Rentz, new species, by monotypy.

DESCRIPTION

Head large, not seated in pronotum, cordate in frontal outline. Eye situated high on head, rather shallow, prominent (male) or considerably reduced (female). Labrum longer than broad; mandible obscured by lacinia, only its base visible anteriorly; maxillary palpus elongate, 5-segmented. Antenna short, with 10 articles. Pronotum broader than long, caudal margin not produced not hoodlike, only covering base of tegmen; cephalic and caudal margins both truncate to weakly obtuse, lateral lobes shallow, ventral margin straight; surface of disk relatively smooth, with two oblique lateral impressions, indicated mostly by colour. Prosternum armed with a pair of quadriform plates, divided mesad, then preceded by a pair of lateral sclerites, in turn, preceded by two pairs of linearly arranged setaceous unsclerotized lobiform processes, the more caudal pair more developed and more setaceous; mesosternum with a similar pair of plate-like processes, somewhat larger; metasternum with massive plate-like processes, caudal internal angles acutely produced. Fore coxa enormously enlarged, commencing ventrad of lateral pronotal lobe; middle coxa about half size of fore coxa; hind coxa massive. Fore and middle trochanters small, elongate; hind trochanter larger, quadrate. Fore femur short, laterally flattened, dorso-ventrally expanded, and more emphasized in female. Fore tibia only slightly longer than femur, feebly laterally compressed, not dorso-ventrally flattened; ventral surface with a single spine positioned in the middle, subapically between the two internal spurs; apex with 2 spurs on anterior margin; the more dorsal of which is short, blunt, excavate, ventral spur more aciculate, positioned ventrad of metatarsus; posterior margin with a single, subapical spine and with a pair of much longer spurs, the more dorsal of which is expanded on its dorsal surface, the more ventral more aciculate, its apex directed mesad; dorsal surface unarmed except for minute, short, stout spine positioned on external margin, this spine highly variable in size even on the same individual. Middle tibia unarmed dorsally, elongate, slender in male, short, stout, dorso-ventrally flattened in female; ventral surface with a single aciculate subapical spine positioned ventral to metatarsus;

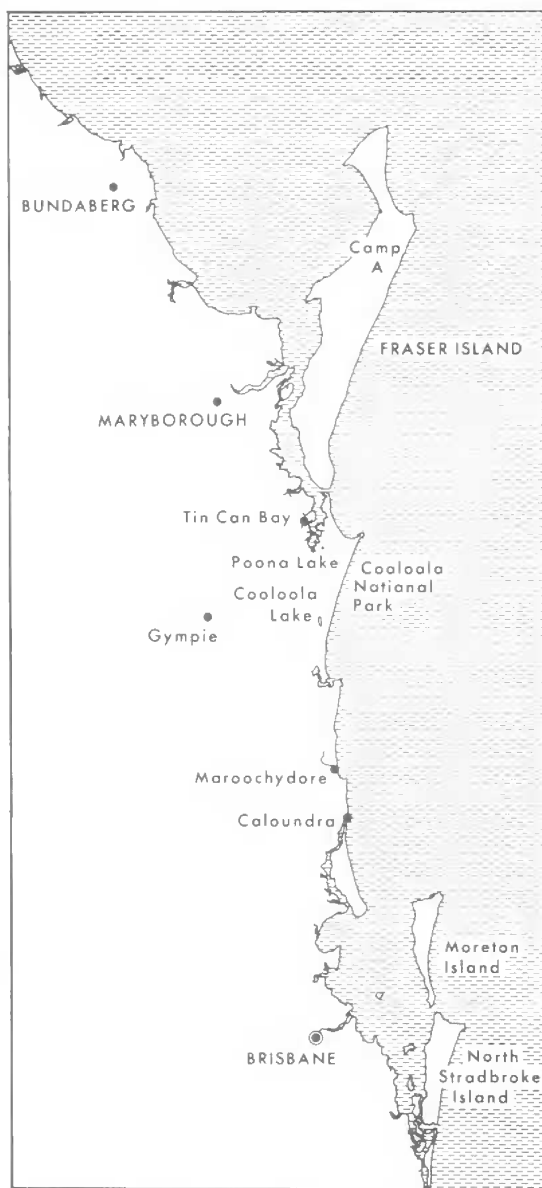


FIG. 3: Map of area inhabited by *C. propator*. See text for discussion.

apex bearing 6 spurs; 3 on anterior and 3 on posterior margin. Hind tibia unarmed dorsally and ventrally; apex with 6 spurs, sexually dimorphic; (male) with 3 on internal, 3 on external margin, most dorsal of internal spurs the largest, spatulate, its internal surface minutely striate, remaining spurs smaller in size, more elongate; (female) all spurs short, broad, apically excavate, surfaces striate, dorso-internal spur, in outline, ovoid, remaining spurs short, stout. Tarsi (male) tarsi elongate, claw well developed; (female) tarsi short. Prothoracic auditory structure absent; metathorax and 6 abdominal segments with well-defined spiracles. Internal surface of hind femur and adjacent portion of abdomen without stridulatory pegs. Dorsal surface of abdomen without median carina. Male terminalia: tenth tergite with a pair of small widely separated hooks; supra-anal plate simple; cercus tubular, apex blunt, not serving a grasping function; paraprocts developed, with apical hook. Subgenital plate bearing styli; no sclerotized concealed genitalia. Female terminalia: similar to male except tenth tergite without hooks, cercus somewhat shorter, more robust, subgenital plate short, supra-anal plate unmodified. Ovipositor short, scarcely projecting beyond abdominal apex, 6-valved. External margins of pronotum, legs, sternum and external ventral margins of abdomen setaceous.

Cooloola propator*, new species
(Figs. 1–14)

MATERIAL EXAMINED

HOLOTYPE: MALE (pinned), Queensland, Cooloola National Park, Rainbow Beach, near Poona Lake, February 1976, V. Davies collector, In pitfall trap, QM T8309.

DESCRIPTION

HOLOTYPE: Internal surface of hind femur and adjacent portion of abdomen without stridulatory pegs; tenth tergite basically unmodified, median portion weakly concave, lateral portions feebly produced; supra-anal plate triangular, minute; paraprocts projecting somewhat from abdomen, not appearing highly mobile; subgenital plate quadrate, fairly short; median portion without incision.

FEMALE: Differs from male in following characters: size larger, form much more robust. Fore, middle, and hind tibiae proportionately stouter, more depressed, thickened; fore tibia rugulose dorsally on external margin at apex;

middle tibia very short, 1.5 times as long as greatest width. All tibial spines more robust, shorter, more blunt, trowel-shaped. Cercus tubular, apically blunt; supra-anal plate triangular. Ovipositor with dorsal valves aciculate, apex highly sclerotized, extending slightly beyond abdomen; internal valves short, stout, obtuse; ventral valves short, broadly triangular, completely concealing internal valves. Colouration: General colour tawny butterscotch brown; nymphs and female pale whitish, with following darker areas; eyes black except dorso-internal angles whitish; tegmen dark brown, veins somewhat darker; dorsal surface of pronotum with irregular brownish patches; outer pagina of hind femur with faint whitish herringbone pattern; apices of all spines and spurs dark brown or blackish; ventral surface of entire insect pale, thoracic portions darker. Nymphs and female (subadult?) almost white except for eyes and spines.

PARATYPES: 1♂, Queensland, Cooloola National Park, 7 km NE of Lake Cooloola, mid-Oct. – mid-Nov. 1978, K. Plowman, in pitfall trap QM T8310. 1♂, Freshwater Lake, 25 Oct. 1978, R. Nicholas, ANIC collection, Canberra. 1♀, Freshwater Lake camping area, 30 Oct. 1978, M.R. Johnston, QM T8311. 1 nymph, 25° 10'S 153° 17'E, 19 km SSW of Indian Head, Fraser Island, National Park headquarters, Camp A July 1978, T. Bade, QM T8312. 1♀, 1 km S of Freshwater Lake Camping area, 4 Aug. 1979, P. Nicholas, QM T8313. 1♂, 1.6 km N of Rainbow Gorge, Fraser Island, 5 Oct. 1979, R. Perry, QM T8319. 5♂♂, Freshwater Camp Ground, Cooloola Nat. Park SE. Qld., 4.v.1979 – 29.i.1980, G.B. Monteith, ex guttertrap, open forest, 2 in QM (T8389 & T8390) and 3 in ANIC.

RELATIONSHIPS

The peculiar combination of characters exhibited by *C. propator* makes it difficult to determine its relationships. The presently accepted conservative classification of the Orthoptera (see Key, 1970, for example) recognizes two suborders. This division is based primarily on the number of antennal segments, 30 or more = Ensifera, i.e. katydids and crickets; 30 or fewer = Caelifera, i.e. grasshoppers, pygmy mole crickets, cylindrachetids. Were *C. propator* to have antennae with more than 30 articles, it would unquestionably be placed in the Ensifera. Its habitus is not unlike that of several of the families included therein. And the structure of the ovipositor, also of critical importance, seems within the range found in the Ensifera. I am considering the Cooloolidae as very aberrant ensiferans in the Gryllacridoidea.

*Denoting first of a kind.

TABLE 1: MEASUREMENTS (IN MM), MAXIMUM DIMENSIONS OF EACH APPENDAGE

	holotype	paratype (male)	paratype (male)	paratype (female)
Length body	23.2*	29.0	27.0	30.0
Head: depth	8.7	9.3	8.1	11.5
width	6.5	7.0	7.0	7.8
Length fore leg:				
femur	8.1	7.3	8.1	7.5
tibia	7.5	7.6	7.0	6.5
tarsus	8.8	7.2	X	4.0
Length middle leg:				
femur	6.5	7.3	6.5	7.0
tibia	6.0	5.8	5.4	4.7
tarsus	8.7	7.4	7.5	5.1
Length hind leg:				
femur	11.0	11.3	10.5	10.0
tibia	9.0	8.2	8.0	7.0
tarsus	9.8	9.8	9.0	6.8
Pronotum:				
length	5.2	6.2	5.5	6.5
width	7.5	7.7	7.7	7.1
Length lateral lobe	4.4	4.7	4.2	6.4
Length tegmen	6.4	7.1	5.3	—

*Length of body of holotype reduced because specimen is pinned, and abdomen shrunken. All others in alcohol.

Table 2 presents characters of evolutionary importance in the more closely related ensiferan families (the Grylloidea are excluded since they possess 3-segmented tarsi and a 4-valved ovipositor. These primary characters are not borne by any of the examples in Table 2. Similarly, the Tettigoniidae are excluded because most members possess a tegminal file-scraper apparatus and tibial auditory apparatus, characters, in combination, not shared by any of the listed families). The data in Table 2 indicate that there is little similarity between the Cooloolidae and either the Gryllacrididae or the Rhaphidophoridae.

I have had the opportunity to study the male type of the type species of *Oryctopus*, *O. bolivari* Brunner (Paris Museum) and the types of the following species of the genus: *O. prodigiosus* Bolivar, *O. bouvieri* Karny, and *O. lagenipes* Karny all in the collection of the Paris Museum. An additional subadult female apparently taken with the type of *O. prodigiosus* was sent to me

from the Vienna Museum. The above species were described from the Madras area of southern India. An additional species, *O. sordellii* Griffini, not seen by me, is known from Ceylon. Not all of these species are generically related. For example, *O. lagenipes* was described without locality data. It is a late instar nymph of some other genus, perhaps the American *Stenopelmatus*. It was reported to have single-segmented antennae, but the type clearly shows this is the result of breakage. Additionally, *O. lagenipes* has mandibles typical of most stenopelmatus. The species is definitely misplaced in *Oryctopus*. The female of *O. prodigiosus* was reported to be antenna-less, but my examination of the subadult female indicates that they have been broken at the bases.

With the exception of *O. lagenipes*, the above-mentioned *Oryctopus* species show remarkable similarity in a number of characters to *Cooloola propator*. Both genera are adapted for burrowing. The legs are shortened and muscular, the spines are excavate, but in *Oryctopus* they are sharply pointed. Both genera are very pale in colour. Adult males are brachypterous or micropterous, females are apterous. The antennae are reduced in length and segment number, and although some of the types of *Oryctopus* have broken antennae, those that are entire are clearly reduced in size and segment number. The eyes of both genera are reduced, and in both this is sexually dimorphic with females showing greater reduction in the number of eye facets and in overall size of the eye. The tarsal claw of both genera is greatly reduced in females but is normal in males. On external appearance the two genera are remarkably similar (compare Bolivar's 1899 figs. 21, 21a, 21b, and Karny 1932, figs. 25, 26 with those presented here).

Detailed closer examination reveals a wide dissimilarity between the two genera. The tarsi of *Oryctopus* species are typically stenopelmatus. They are distinctly laterally compressed and the metatarsus is very elongate, longer than the remaining tarsal articles combined. In *Cooloola* the tarsi are depressed and not laterally compressed. The metatarsus is short. The mouthparts of the two genera are extremely different. As normal in the Orthoptera, the mandibles of *Oryctopus* are larger and more prominent than the lacinia of the maxilla. The reverse is true in *Cooloola*. In the latter, the mandible is not lanceolate (see Fig. 10), whereas in *O. prodigiosus* the mandible is lanceolate, without any dentition, very similar in shape to the lacinia. This cutting type of mandible in

Oryctopus appears unique in the Orthoptera. At the base of the lacinia in *Oryctopus*, several stout bristles occur; these are absent in *Cooloola*.

The tremendous expansion of the thoracic region reflected in *Cooloola* (Fig. 1) has not occurred in *Oryctopus*. In this respect, *Oryctopus* is similar to such burrowing genera as *Stenopelmatus* where the base of the legs is inserted just under the lower margin of the lateral

lobe of the pronotum. In *Cooloola* (Fig. 1), the thoracic region has expanded dorso-ventrally greatly separating the base of the legs from the ventral margin of the lateral lobe of the pronotum. The sternal plates described for *C. propator* are wholly absent from *Oryctopus*. The male terminalia are quite dissimilar. In the male of *O. prodigiosus* before me, the subgenital plate is reduced, its apex acute and without styli. The cerci are erect and conical and apically digitiform.

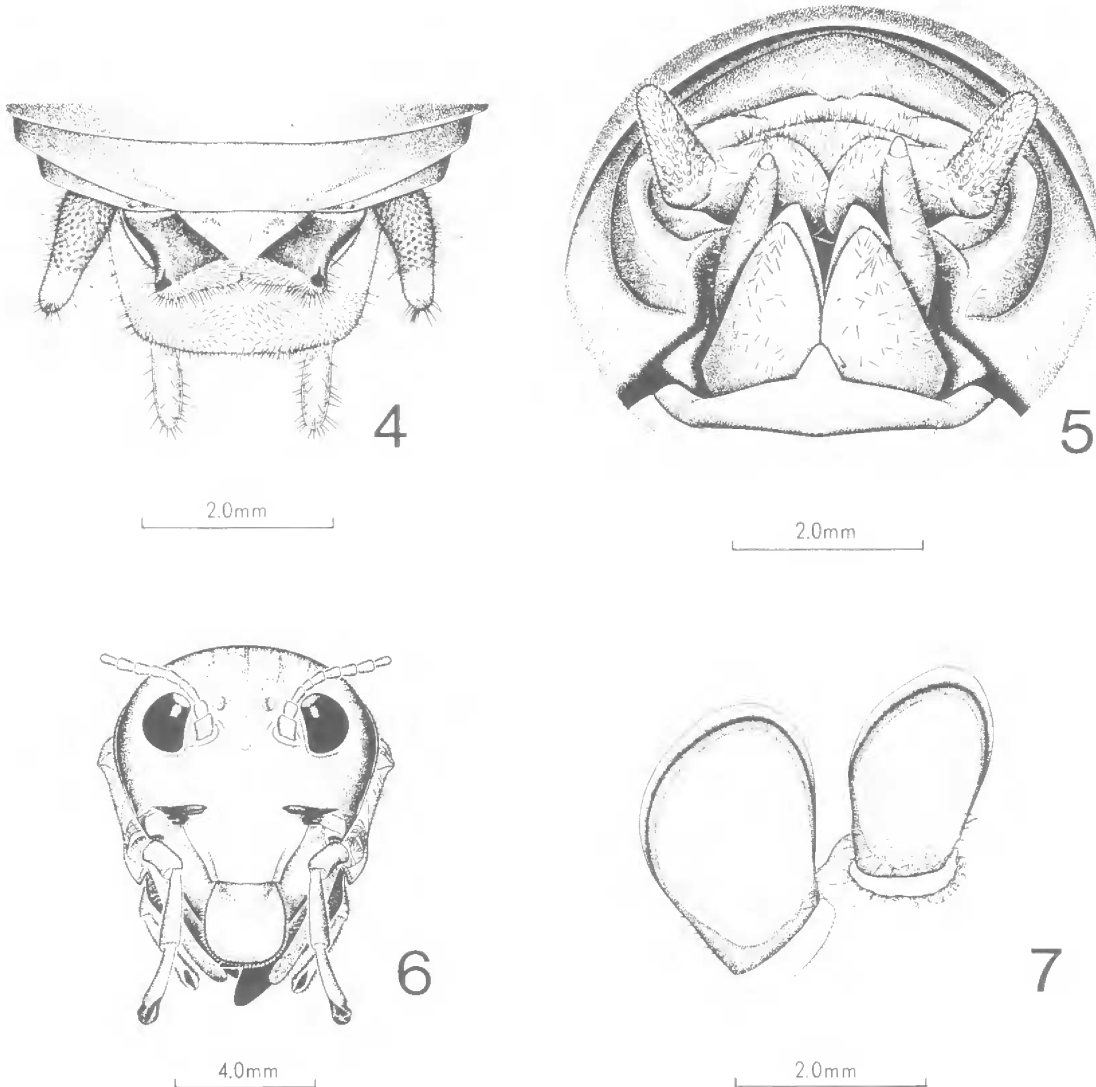
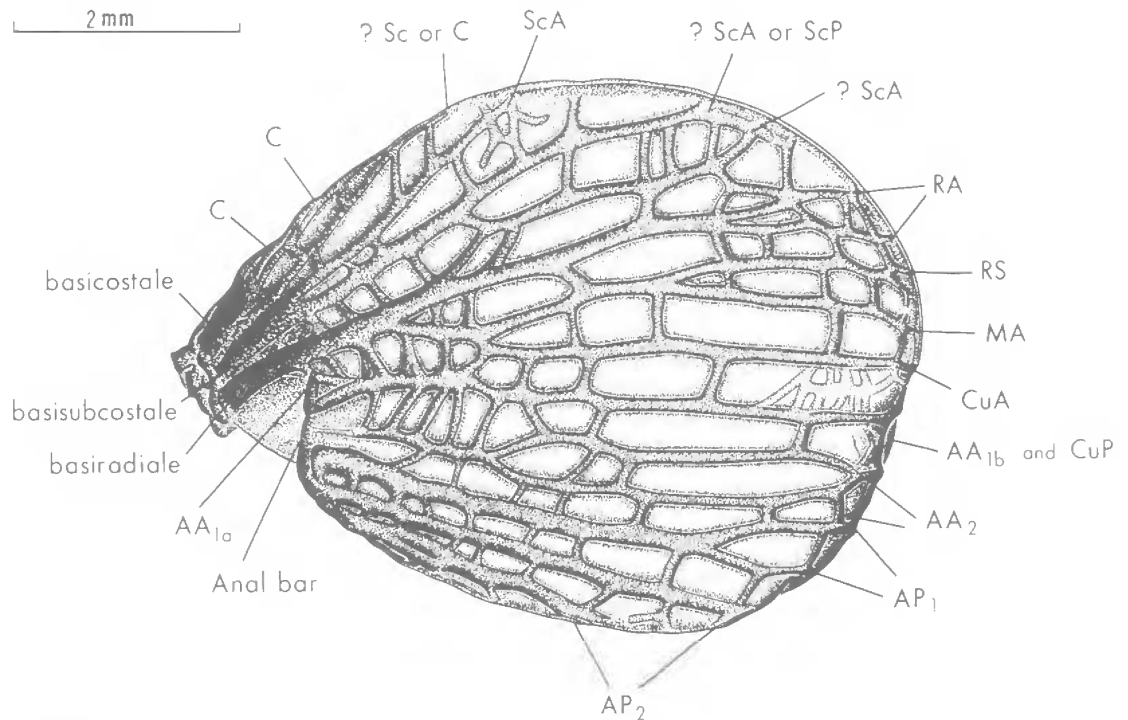


FIG. 4-7: Diagnostic structures in *C. propator*. 4, dorsal view, male terminalia; 5, caudal view, female terminalia; 6, frontal view, head of paratype male: note protruding lacinia; 7, internal view, apical spurs left tibia, female: note striations.

TABLE 2: CHARACTERS THOUGHT TO BE OF EVOLUTIONARY IMPORTANCE IN SEVERAL ENSIFERAN FAMILIES.

CHARACTER	GRYLLACRIDIDAE	RHAPHIDOPHORIDAE	STENOPELMATIDAE	COOLOOLIDAE
Antennal sockets	widely separated	nearly touching	widely separated	widely separated
Fastigium of vertex	flat or convex	sulcate or strongly compressed	convex or sulcate	flat, not sulcate
Lacinia	with 2 hook-like processes	with 3 hook-like processes	with 2 spiniform processes 1 minute	without any appendages
Tarsi	depressed, lobate	compressed, sclerotized, often with a minute pulvillus apically	compressed, pulvillate	compressed, pulvillate
Metatarsi	depressed, pulvillate	compressed, sclerotized	compressed with 2 pulvilli	feebly compressed, with 2 pulvilli
Tibial auditory tympanum	absent	absent	present or absent	absent
Wings	apterous or alate	apterous	great majority of species apterous	sexually dimorphic, males brachypterous
Sclerotization of tegmina	tegmina and wings soft, flexible	—	tegmina toughened	tegmina toughened
Femoro-abdominal stridulatory apparatus	present	absent	present	absent
Inserting angle of hind femur	present	absent	present	present, but minute

FIG. 8: Right tegmen of *C. propator*. Nomenclature after Kululova-Peck (1978).

The apex of the abdomen and the paraprocts are not modified but there are 2 pairs of digitiform hook-like, lightly sclerotized appendages on the genital orifice. These appendages are absent from *C. propator*.

In summary, it appears that *Oryctopus* is only superficially similar to *Cooloola*, the similarities being apparently associated with adaptation to a wholly fossorial habit. Since *Oryctopus* seems stenopelmatid in all but a few characters (most notably the reduced number of antennal articles and the piercing or cutting mouthparts) I feel that it should remain in the Stenopelmatidae, with the reservation that examination of additional material might lead to a change of its placement but that this would not affect the classification of the Cooloolidae.

COMPARATIVE MORPHOLOGY OF SELECTED STRUCTURES IN THE COOLOOLIDAE

WING VENATION: The brachyptery and modification of the tegmen render identification of the veins difficult. A drawing of the tegmen was examined by Dr J. Kukalova-Peck who stated (in litt.) that she found it difficult to trace the homologies of the veins because of the sclerotization at the base of the tegmen. As a result, the origin of several of the veins is obscure. Some of the problems are as follows: it is not possible to determine with certainty whether ?C or Sc starts from the basicostale (and is therefore a part of the costal system) or from the basisubcostale (and is therefore part of the subcostal system); similarly with ?ScA or ScP the three branches may, in fact, be all ScA. In Figure 8 the veins in doubt are labelled with a query.

The venation of *C. propator* does not reflect relationship with any of the Haglidae, e.g. *Cyphoderris monstrosa* (see Sharov, 1971, fig. 25). Dr Kukalova-Peck feels that the venational characters are quite different and *C. propator* shows more primitive characters in the subcostal system but, conversely, reflects more advanced specialization in the anal field. The strong anal bar which is not present in the Haglidae, indicates that this area was more strongly developed in the past for some purpose, perhaps flight, burrowing, or courtship, but I am not now able to determine it. In sum, it can be stated that the venation of *C. propator* is quite distinct from that of any of the presently known orthopteroids and may indicate that the species is the sole survivor of a very archaic line of hitherto unknown orthopteroids.

MOUTHPARTS: Mouthparts in Orthoptera, though variable, show adaptive modification based on the food preferences of the groups involved. Such was demonstrated by Gangwere (1965) for the North American Orthoptera. The mandibles of each subfamily, and often in groups below that level, are usually distinctive. Of all the mouthparts, the labium appears to remain relatively constant throughout the Orthoptera. The maxillae and labrum show a lesser degree of modification with the maxillae showing more substantial differences than the labrum (*contra* Isely, 1944, who stated that only mandibles show significant adaptive modification).

Because of the conservative nature of mouthparts, they can serve as a character for taxonomic differentiation. Gangwere (1965) was able to show that the tettigoniid subfamilies Conocephalinae, Copiphorinae, and Decticinae were more similar in the morphology of mouthparts, than to the Phaneropterinae of Pseudophyllinae. Such is an accepted fact based on more usual morphological characters.

Gangwere (1965) listed six kinds of mandibles for the Orthoptera. According to his scheme, *C. propator* fits the Carnivorous-Forbivorous or Flesh-Forb feeding subtype. The mandible is elongate and hook-like. The incisor and molar dentes are well defined and sharp, with the latter surrounding a minute but distinct concavity. However, his name of the subtype cannot be applied to *C. propator* since it appears unlikely that this insect feeds upon forbs. It is more probable that it feeds upon roots or organisms encountered underground. Other burrowing Orthoptera, such as mole crickets, have mandibles which are short and stout. They have well-defined molar regions designed for chewing rather than holding or tearing and they are classed in the Omnivorous category.

The mouthparts of *C. propator* are unique among the Ensifera in that the maxillae are larger and more prominent than the mandibles. The galea is small and slender and, as usual in Ensifera, lies above the lacinia. It is shorter than the lacinia, not apically modified and bears two rows of setae dorsally. This is in contrast to the Stenopelmatidae, Rhaphidophoridae and Gryllacrididae. In the first the galea is usually short and broad (see previous discussion for *Oryctopus* as exception). In the raphidophorids and the gryllacridids the galea is massive and its lateral and apical margins overhang the lacinia. The galea is a robust, quadrate structure and in the gryllacridids it is apically modified into a

sclerotized papillate sensory organ as is found in the Tettigoniidae. Laterally the galea possesses well-defined, although irregular, rows of setae.

The peculiar knife-like structure of the lacinia of *C. propator* (Fig. 9) is very different from that of the three related families. The lacinia of *C. propator* is unique in that it is modified to form a

simple, broad, knife-like structure and bears no appendages. The dorsal surface has two minute tubercles at its broadest point, on the internal margin. Lateral to the tubercles lies a pair of pits, the internal pit is large and circular, the external minute. The apex of the lacinia is a smoothly bent cutting edge without hooks or teeth. Apically it is

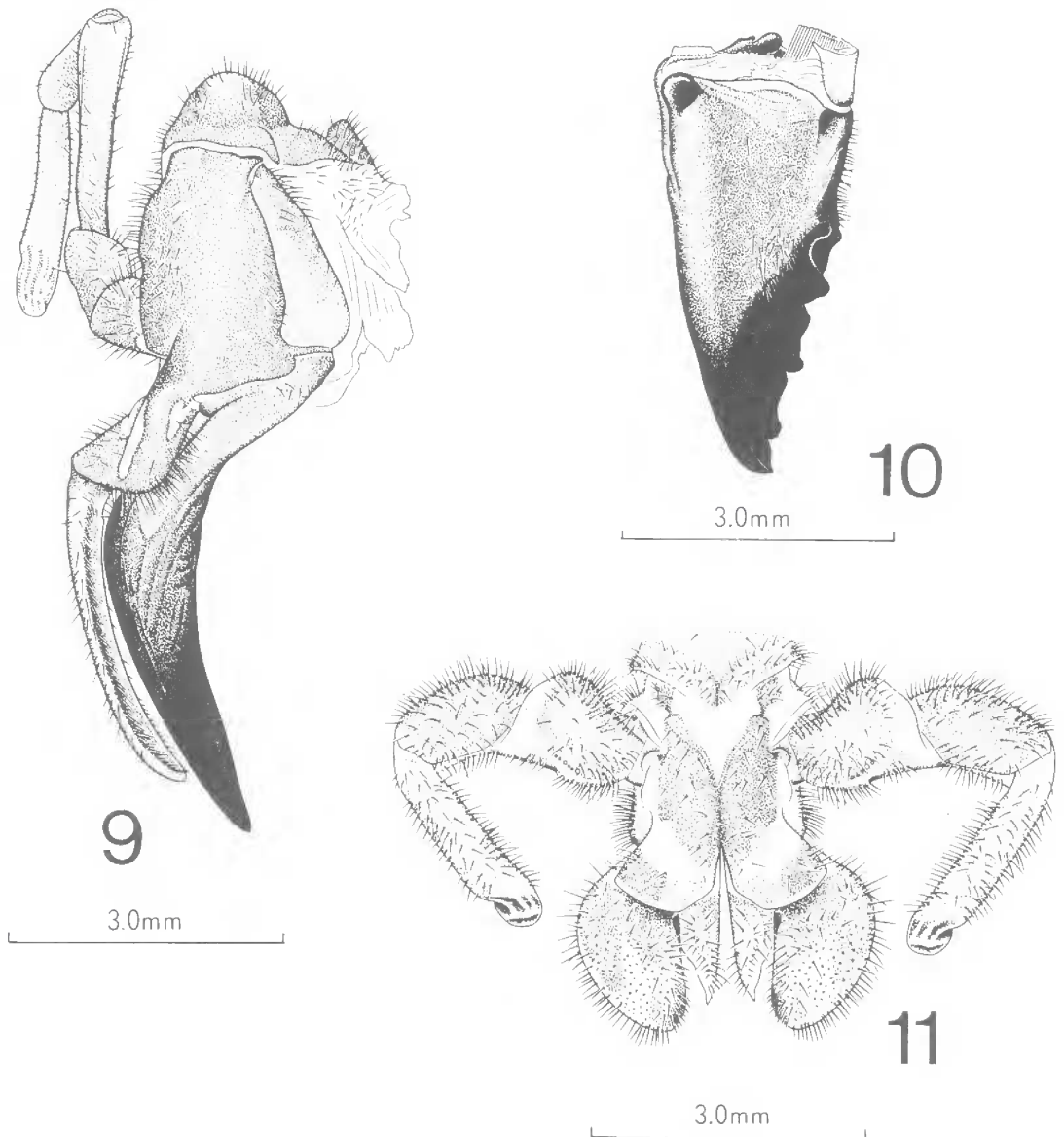


FIG. 9-11: Mouthparts, male paratype *C. propator*. 9, left maxilla: note blade-like lacinia; 10, left mandible: note elongate shape for grasping or tearing; 11, labium.

distinctly spatulate. In length it is half as long again as the mandible.

In the stenopelmatids the lacinia is dorsally tuberculate on the internal margin and bears at least two large tubercles on its dorsal surface. There is an elongate spiniform tooth on the internal margin at the base of the apical portion. A tiny spiniform tooth is found on the internal cutting edge of the lacinia itself. In the raphidophorids, the lacinia bears no tubercles and has three apical teeth. It shows no modification for cutting, but appears to have a tearing, or perhaps a sorting, function. The gryllacridids have an elongate non-tuberculate lacinia bearing two apical teeth on the internal margin. Near the proximal tooth lies an inconspicuous, short, stout spine.

The labrum and labium (Fig. 11) appear similar to those of other Orthoptera.

In general, the mouthparts of the Cooloola Monster suggest adaptation for piercing and chewing rather than chewing only, as is normal for Orthoptera. The reduced nature of the molar area (Fig. 10) and extraordinary development of the lacinia relative to the mandible supports this hypothesis. The structure of the gut also supports it. The enlarged foregut (see below) may be a modification for storage of liquid food and may explain the absence of solid food from the foregut in field-collected specimens. The reduced armature of the proventriculus may reflect its lessened function as a sieving mechanism. One can only speculate that the insects feed on insect larvae or, perhaps earthworms which are abundant in the habitat, or may feed on the toughened roots of trees and shrubs which lace the habitat.

THE ALIMENTARY TRACT: The alimentary canal was removed from one of the fluid-preserved specimens and studied as described by Judd (1948). For the sake of comparison, the terminology of structures follows that of Judd and his code is used in my illustrations. The alimentary canal of *C. propator* is peculiar in that the crop is extremely long and convoluted. The proventriculus lies in the posterior part of the abdomen, thereby by necessity, severely limiting the length of the midgut and hindgut. Although this is common in gryllacridids, stenopelmatids and *Cyphoderris* (Haglidae), it is not normal in tettigoniids or raphidophorids. In those families, the proventriculus lies in the thoracic region. Strangely, these differences were not registered by Judd. Perhaps some stenopelmatids, the cooloolids and *Cyphoderris* are sporadic and opportunistic

feeders, feeding only occasionally when the situation warrants it, and then consuming large quantities of food.

Evidence suggests that sporadic feeding may depend on local weather conditions. Many of these insects are extremely sensitive to dry conditions and all are nocturnal. They may not venture forth each night unless atmospheric conditions are suitable. Such an explanation was offered for several species of the hemicine stenopelmatid *Cnemotettix* of California which spend periods of dry weather in their burrows (see Rentz and Weissman 1973). At the same time Rentz and Weissman noted the extraordinarily large size of the faecal pellets of *Cnemotettix*. Curiously, however, I have found that the faecal pellets of certain other stenopelmatids and gryllacridids are very large. The same was also mentioned by Richards (1973, p.226) in the deinacridine stenopelmatid, *Hemideina* spp., the giant weta of New Zealand.

Comparative studies of the proventriculi of several examples each of the Tettigoniidae, Raphidophoridae, Stenopelmatidae, Gryllacrididae, Haglidae (*Cyphoderris*) and Grylloidea indicate that there is considerable overlap in the morphology of this structure from one group to the other. It appears that the taxonomic value of the proventriculus may lie at the generic level. However, a few generalisations can be drawn.

Based on the characters of the proventriculus, the Cooloola monster shows no similarities with any of the Grylloidea. In this group the median tooth normally has lateral projections and two lateral lobes. This is a more complex picture than exists in the Tettigoniodea and Gryllacridoidea. In these groups the general structure is simpler, the lateral teeth and inner barbate lobes of the sclerotized appendage of the proventriculus are absent. It thus seems that, on the basis of this structure, Sharov (1971) was wrong to transfer the Haglidae from the Tettigoniodea to the Gryllodea (= Grylloidea). He did this primarily on wing venation. Fresh preparations of the proventriculi of a species of the two extant genera of the Haglidae show none of the typical gryllid characters. Judd (1948), in an extensive survey of the Orthoptera, made a point that the Raphidophoridae were distinct in that the median tooth of the sclerotized appendage of the proventriculus always bore a tuft of hairs. He illustrated this with several genera. However, I found in the raphidophorid *Macrobaenetes valgum* (Strohecker), a more or less typical example of the family from the southwestern

United States, there are no hairs at all. The lateral lobes, however, are lightly sclerotized as Judd indicated. He considered the proventriculi of the Stenopelmaticidae, Tettigoniidae, and Prophalangopsidae (= Haglidae) indistinguishable from one another at the family level. With this I concur.

The most striking similarity of the proventriculus of the *Cooloola* monster is with that of *Cyphoderris monstrosus* Uhler. Judd did not illustrate an entire section of one of the longitudinal folds of the proventriculus of this important insect, but if he had it would have looked much like Fig. 13. He did illustrate the sclerotized appendage of the proventriculus (Judd 1948, figs. 73, 74) and the similarity with my Fig.

14 is, indeed, astounding. The most obvious differences between the proventriculus of *Cyphoderris* and *Cooloola* are the following: proportionally smaller size of proventriculus in *Cooloola*; much lesser degree of sclerotization; lack of distinct protuberances or modification of the cushions (Fig. 13) (C) of the sclerotized neck region in *Cooloola*; presence of tubular neck region in *Cooloola* (in *Cyphoderris* this is absent and the sclerotized portion of the neck is contiguous with the main portion); more angulate projection of the caudal portion of the barbated lobe (BL) in *Cyphoderris*; more lightly sclerotized loop of hairs (CT) in *Cyphoderris*. It can be concluded that in all aspects of the structure of the

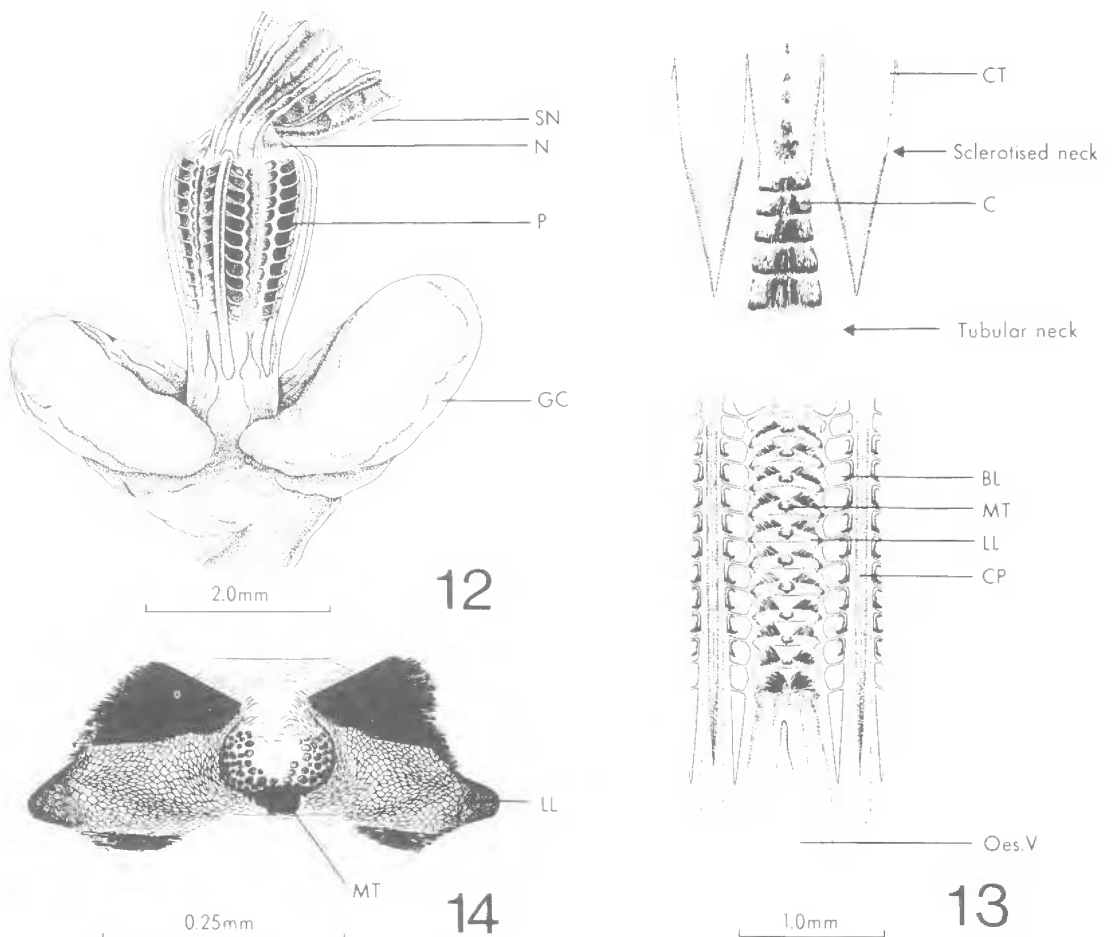


FIG. 12-14: Structures of foregut. Nomenclature after Judd (1948). 12, proventriculus, posterior end of crop and anterior end of midgut. SN = sclerotized neck, UN = tubular neck, P = proventriculus, GC = gastric caeca. 13, sclerotized portion of one longitudinal fold of proventriculus, CT = V-shaped loop of tubercles, C = cushion, BL = barbated lobe, MT = median tooth, LL = lateral lobe, CP = sclerotized partition, Oes.V. = oesophageal valve. 14, sclerotized appendage of proventriculus. LL = lateral lobe, MT = median tooth.

proventriculus, *Cooloola propator* shows more similarities with *Cyphoderris monstrosa* than any other ensiferan.

The proventriculus of *C. propator* is 2.2 mm long, and globular, it is joined to the crop by a tubular neck which is a distinctly unsclerotized zone. Where joined to the midgut, it is surrounded by two moderately large broad gastric caecae (GC). Beyond the constricted neck there are 5 or 6 longitudinal rows (Fig. 13) of poorly defined cushions composed of hairs. Each row of cushions appears faintly divided down the middle and consists of 5 well-defined pairs preceded by 3–5 smaller more poorly defined ones. The anterior cushions bear fewer hairs and are narrower. There is no median projection from any of the cushions. Between each row of cushions there is a V-shaped loop (CT) composed of minute tubercles. Each of the 6 longitudinal folds of the main part of the proventriculus consists of 10–12 sclerotized appendages. The median 5–9 are the widest and best developed, those on either end decreasing in size. Each longitudinal fold is separated by a weakly sclerotized partition (CP) at the end of which there is a fleshy flap of the oesophageal valve (Oes.V.) which is not clothed with hairs. Each median appendage (Fig. 14) has a median tooth (MT) with minute tubercles at the base. There are no lateral teeth. From the side of each tooth are rows of extremely fine setae. Lateral to the seta is a minute blunt lateral lobe (LL). Each lateral lobe is bounded by a larger more quadrate barbed lobe (BL) which bears a blunt tooth posteriorly.

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